tween the Auchenia weddelli Gerv. and the Eschatius conidens, having just about the dimensions of the Camelus dromedarius or the Palaucheria magna Ow. It difters from the Eschatius conidens in the much longer inferior diastema, longer, coössified symphysis, and smaller true molar teeth; the comparison being made with superior molars of the E. conidens.
The alveolus of the inferior canine tooth is small, and is a short distance posterior to the third incisor, being separated by a short diastema. The mental foramen is very large, three times the size of that of the E. conidens, and its anterior edge is 20 mm . posterior to the canine alveolus. The alveolar parapet of the diastema is not so elerated as in E. conidens, but is distinct. The dentition shows that the animal is an old one. The fourth premolar has two divaricate roots, which spread nearly as far anteroposteriorly as those of the first true molar. The crown is compressed. Apex broken. The crowns of the molars are worn; that of the first to the roots. The heel of the third true molar is lost.

$$
\begin{aligned}
& \text { Measurcments. M. } \\
& \text { Width of mandible at inferior canines. . . . . . . . . . . . . . . . . } 027 \\
& \text { Length of inferior postcanine diastema.................. . . . } 110
\end{aligned}
$$

From the Oregon desert ; Professor Condon's collection.
BOS Liun.
Bos latifroxs Harlan.
This species is represented by numerous remains, and must have been abundant in Mexico during the Pliocene epoch.

On the structure of the feet in the Extinct Artiodactyla of North America. By E. D. Cope.
(Read before the American Philosophical Society, August 15, 1854.)
The structure of the feet of a number of the Artiodactyles of the Tertiary beds of North America has already been described. In this paper I enumerate these, and add descriptions of some types which have been hitherto unknown. I commence with the Bunodonta.

## Bunodonta.

Pantolestes Cope.
The structure of the tarsus only of this Eocene genus is known.*

[^0]The cuboid and navicular bones are distinct from each other and from the cuneïforms, and the ecto- and mesocuneïform are coössified. There are four metatarsals. The laterals (ii and v) are slender; and the medians are distinct but appressed, their adjacent sides being flattened. This foot structure is remarkably advanced considering the early age, Wasatch Eocene, of the period of its existence, and the primitive, tritubercular bunodont character of the superior dentition. The selenodont types which appear first in our series of formations, the Oreodontidæ of the White River low Miocene, present a much more primitive type of foot. The camel series is remarkable for the early and continued absence of the first and fifth metapodial bones. The first known of the line, Poëbrotherium, from the White River beds, has only minute rudiments of them. It is probable the Pantolestes, or some member of the Pantolestidæ, is an ancestor of Poëbrotherium, with a number of lost types intervening.

Elotherium Aym.
The first information respecting the structure of the feet of this genus was furnished by Marsh.* He says "The radius and ulna were separate or very loosely united. The third and fourth metacarpals were nearly equal in size, and the scond and fifth longer than the corresponding bones of the pes. In the latter the first digit was wanting, and the fifth rudimentary." This deseription leaves us in the dark as to the development of the second digit in the posterior foot and of the second and fifth in the anterior foot. The ambiguous language led me to infer that there are four digits of the anterior foot of the animal described by Marsh, and hence to separate it generically from Elotherium. The first definite information is derived from Kowalevsky, from his great memoir on the genus Anthracotherium. $\dagger$ He here states distinctly that the genus is bidigitate, but with small rudiments of the second and fifth metapodial bones. He shows also that the lunar is equally supported by the magnum and unciforum. In a memoir especially devoted to this genus $\ddagger$ he also shows that the cuboid, navicular and cuneiforms are distinct, while the ecto- and mesocuneïforms are coösified, the entocuneif form being absent. The structure of the tarsus in this genus is then as in Pantolestes, and from this genus or one of the same family, Elotherium no doubt took its origin through intermediate genera. ||

## Selenodonta.

## Oreodon Leidy.

We owe to Leidy the following statement regarding the foot structure of this genus. § What are supposed to be the bones of the forearm and leg

[^1]are discrete, as in the log ; and the bones of the feet correspond in number with those of this animal. In 1873, Professor Marsh confirmed these statemeuts as regards the metacarpal bones,* and added "that the navicular and.cuboid bones were loosely coösified or separate." In $1884+$ I gave a full accomnt of the structure of the limbs in this genus. I mentioned a peculiar feature of the carpus, viz.: that the os lumare is supported below by the inward extension of the unciform, so that the magnum is below the scaphoideum. I also showed that the cuneïforms are distinct, and that the entocuneiform is wantung.

Eucrotaphus Leidy.
I have already stated that this geuts is tetradactyle anteriorly and pos. teriorly. $\ddagger$ I now add that the structure of the limbs and feet is in other respects like that of Oreodon. This is true of the inner extension of the unciform, so that the magnum is below the trapezoïdes. The inner side of the latter bone in the Eucrotaphus pacificus, is so excavated, that there was plainly a free trapezium of small size. In the posterior foot the entocuneïform is wanting, and the mesocuneifform is distinct from the ectocuneïform.

## Merycochierus Leidy.

The first information of the foot structure of this genus is contained in my paper on the Oreodontidæ above cited. \| The fore and hind feet are there stated to be tetradactyle. I now add that in the M. montanus Cope. the os magnum is entirely below the scaphoid, and that there is a distinct trapezium. The posterior foot is constituted as in Eucrotaphus; I also observe that the navicular has a peculiar little facet on its distal face near the front of the external edge. This fits a corresponding facet which forms the proximal surface of a ledge, which extends from front to rear on the inner side of the cuboid. In Eucrotaphus pacificus the arrangement is similar, excepting that the ledge of the cuboid is interrupted at the middle by a deep excavation. In Merychyus arenarum the cuboid is like that of Merycocherus montanus in regard to this letge.

## Merchyus Leidy.

The limbs and feet in this genus are quite as in Merycochœrus. The species which I have examined is the M. arenarum Cope.

Leptomeryx Leidy.
We possess as yet no information regarding the limbs and feet of this genus. It is therefore fortunate that I obtained in the White River bed of North Eastern Colorado, in 1879, a nearly entire skeleton of the $L$. evansi Leidy. The bones were all found close together, and belong to two individuals, and are without admixture of those of any other species.

[^2]From these, and inferentially from other specimens, is derived the curious fact, that there are four distinct metacarpals, all supporting digits, while there are but two metatarsals, which are coösified into a cannon bone. This diversity between the limbs is unparalleled, although an approach to such a condition is seen in the peccary. In this animal, as is well known, there are four distinct digits in the manus, while in the pes, the metatarsals are coössified proximally, and the fifth metatarsal is reduced to a scale. This difference between the two limbs is a further illustration of Mr. Ryder's statement that the posterior limb is in advance of the anterior in grade of development, for which I have endeavored to account by reference to the fact that it is the posterior foot which receives the greater number of impacts in progression. This is because the hind limb is the principal propeller of the body.

In accordance with the structure of the fect, the fore-limb is much behind the posterior limb in the fixity of its parts. The ulna and radius are distinct ; the head of the latter a regular transverse oval. The distal extremity of the fibula is not coössified with the tibia, but forms a separate bone, as in the Ruminantia.

The lunar is mainly supported by the unciform, so much so that the front face of the magnum is not beveled to fit the former. Behind the face, the edge of the magnum is a little beveled for the lunar; but the former bone lies almost entirely under the scaphoid. The trapezoilles is coössified with the magnum. No distinct trapezium.

The cuboid and navicular are solidly united. The ecto- and mesocuneïforms are distinct, and there is no entocuncïform. The second metatarsal is represented by a flat oval bone which is borne on the underside of the projecting heel of the third metatarsal. The fifth is of smaller size, and is a scale imbedded in a depression of the posterior part of the side of the fourth. Ungues unilateral, trihedral and acute.

## Hypertragulus Cope.

Remains of this genus are as abundant in the White River beds as are those of Leptomeryx, and like that genus I know but the one species, the II. calcaratus Cope. Unfortunately I have not been able to obtain bones of the skeleton connected with dentition from this formation, although numerous bones occur separately which probably belong to it. The genus is however abundantly represented in the Johu Day Miocene beds of Oregon, where Leptomeryx does not probably occur. At least no specimens of the latter are to be found in a collection of between one and two hundred individuals of this general type in my collection. I cannot distinguish the John Day species from the $H$. calcaratus, althongh the size is generally distinctly larger.* In other cases the size is the same. To the John Day specimens then I refer for the characters of the feet of this genus.

[^3]The ulna and radins are coösified. The scaphoid and lunar facets of the radius are well distinguished by an oblique ridge. The carpus is unknown. Tbe median metacarpals are separate; whether the second and fifth are well developed I do not know, but suspect them to be so, as in Leptomeryx, since the third and fourth bear no adherent rudiments. The cuboid and navicular bones are united, while the cuneifforms are distinct from them and from each other, as in Leptomeryx. There are but two developed metatarsals, and these are distinct from each other. Thus the fore-limb in its ulno-radius exhibits a little advance over Leptomeryx; while in the separate metatarsals it is behind the latter.

## Hypisodus Cope.

This genus is remarkable for its prismatic dentition, being the only Artiodactyle presenting the character in the White River fanna.* It was probably well advanced in foot characters, but of these I know but little. Parts of two tarsi found with the jaws of the H. minimus Cope, are referred to the species on account of their very small size, and general correspondence. The cuboid and naricular are coössified. Their distal face, especially the navicular part, is so narrow transversely, that it is almost certain that the third and fourth metatarsals are coössified, and that the second and fifth are rudimental or wanting. There is no trace of facets for the latter on the naviculo-cuboid.

Poebrotherium Leidy.
I have fully described the limbs of this genus in the Annnal Report of the U. S. Geological Survey of the Territories for $1873+$, as seen in the $P$. vilsoni Leidy, from the White River beds, and have confirmed them from a fine specimen of the $P$. sternbergi Cope, from the John Day or Middle Miocene of Oregon. $\ddagger$ The characters are; ulna and radius coössified; trapezium and trapezoïdes present and distinct; magnum supporting part of lunar. Two distinct metacarpals, scales representing the second and fifth ; navicular and cuboid bones distinct, as are the ecto- and mesocuncïforms; entocuneïform wanting. Metatarsals two, distinct ; second and fifth represented by scales.

## Observations on tile Phylogeny.

I have maintained $\|$ that the selenodont dentition is a derivative of the bunodont, a proposition which seems unavoidable from a mechanical point of view. The testimony of palaontology is also in its favor, since in America the oldest artiodactyle, Pantolestes, is bunodont. Fowalersky in the phylogenetic table given in his monograph of Anthracotheriums does

[^4]not commit himself as to this point, but allows the development of the two types of dentition to appear to have been cotemporary and from some common origin. He then derives from such a common point of departure first, the Hyopotamidæ, which first appear in the Eocene, and second, the ancestors of the Anoplotheriidæ. From the Hyopotamide he derives all the modern Selenodonta, exclusive of the Camelidæ. The latter group he omits from his table, doubtless because his information on the subject was insufficient. The main line of origin of the Selenodonta is divided early in Miocene time, the genus Gelocus giviug origin to the Pecora, and the genus Hyæmoschus to the Tragulina.
In describing the characters of the genus Poëbrotherium for the first time, I remarked as follows :* "The present genus is a more generalized type than Gelocus, and in its distinct trapezoïd and distinct metacarpals represents an early stage in the dexelopmental history of that genus. It also presents affinity to an earlier type than the Tragulidæ which sometimes have the divided metacarpals, but the trapezoïles and magnum coössified. In fact Poëbrotherinm as direct ancestor of the camels, indicates that the existing Ruminantia were derived from three lines represented by the genera Gelocus for the typical forms, Poëbrotherium for the camels and Hyæmoschus for the Tragulidæ."

These views being then established on sufficient evidence, it remains to make such additions as the facts cited in the present paper indicate. First in importance comes the place in the phylogeny of the Selenodonta, of the Oreodontidæ. The peculiar inward extension of the unciform bone already ascribed to them, characterizes also among extinct forms the genus Leptomeryx, and probably Hypertragulus. Among recent ruminants it is ouly seen in the Tragulide. $\dagger$ If we arrange these types in serial order we find the modifications of form to be generally identical with those of the other ruminant lines, in the coössification of the bones of the legs and feet. This series may then be regarded as phylogenetic. The peculiar structure of the carpus of the Oreodontidæ, puts them out of the question as ancestors of any type of existing ruminants other than the Tragulina. Whether they themselves can be traced to a five lobed, or to a four-lobed bunodont ancestor, remains an undecided question. It is not, however, probable that a five-lobed form has been intercalated in a series, both of whose extremities are fotr-lobed. If this be true, the Oreodontidre must be regarded as an ancestral type of Selenodonta, coëqual with the Hyopotamidæ, and it may well be questioned whether the latter can have been ancestors of the existing Ruminantia, whose molars are fonr-lobed.

So the present investigation does not disclose the ancestral stock of the Pecora. In North America we have not progressed further in the solution of this question than I reached in $1877, \ddagger$ after a study of the genera

[^5]Cosoryx Leidy, and Blastomeryx Cope. I had already* suggested that the former genus is the ancestor of the Cervida, but subsequently $\dagger$ remarked: "It is not probable this genus is the immediate ancestor of Cervus, from the fact that the molar teeth display in their prismatic form a higher degree of specialization than belongs to that genus. It is probable that the true ancestor combined the dental type of Cervus with the distinct roots and short crowns of the molars, with the type of horns here described." I at that time included a species (Cosoryx gemmifer Cope) in the genus, provisionally, which has the type of molars in question. Having discovered another, larger species, which has the same type of molars, I at once distinguished the provisional group in which I had placed the $C$. gemmifer, Blastomeryx, as a genus; and in describing the species ( $B$. borealis) observed as follows:
"In brief, its molars differ from those of Cosoryx ("Dicrocerus") much as those of the deer differ from the molars of the antelope. While Cosoryx ("Dicrocerus") was probably the ancestor of Antilocapra, Blastomeryx was the ancestor of Cervus or Cariacus." This opinion expresses all the information I possess on the subject at present. It remains to ascertain the structure of the anterior feet in Hypisodus, which is the earliest genus of Ruminantia known to have prismatic molars.

The following table will represent the views expressed in the preceding pages :


[^6]
[^0]:    * Cope, Proceedings American Philosophical Society, 1881, p. 188. Pal. Bulletin, No. 34.

[^1]:    * American Journal Sci. Arts, 1873, p. 487, June.
    $\dagger$ Palæontographica, 1873, p. 188, August?
    $\ddagger$ Loc. cit., Xxii, N. F. II, 7, p. 415 .
    || I have given the structure of the anterior leg and foot in Elotherium imperator, Bulletin U. S. Geol. Surv. Terrs., Vol v, p. 60.
    \& Extinct Mammalia of Dakota and Nebraska, 1869, p. 72.

[^2]:    * Amer. Jour. Sci. Arts, p. 409 ; Marsh does not credit Leidy with his previous observations.
    $\dagger$ Proceeds. Amer. Philos. Society, Pal. Bulletin, No. 3S, pp. 508-10.
    $\ddagger$ Loc. cit., p. 504.
    \| Proceeds. Amer. Philos. Society, 1884, p. 501.

[^3]:    * It is probably this species that is cited by Leidy as the Leptomeryx evansi in the Report U. S. Geol. Survey Terrs. I, p. 216.

[^4]:    * See Cope, Annual Report U.S. Geological Survey Terrs., 1873, p. 501, where the cuboid and navicular are stated to be united.
    $\dagger$ 1874, p. 499.
    $\ddagger$ Bulletin U. S Geol. Survey Terrs. V, p. 59.
    $\|$ Journal Academy Natural Sciences, 1874. See also Ryder, The Mechanical Genesis of tooth forms, Proceeds. Academy Philada., 1879, p. 77.
    ? 1873 (? 4), p. 152.
    PROC. AMER. PHILOS. SOC. XXII. 11\%. D. PRINTED OCTOBER 22, 1884.

[^5]:    * Bulletin U. S. Geol. Survey Terrs. Vol. i, No. 1, p. 26, Jan., 1874.
    $\dagger$ Among Perissodactyles it occurs in Triplopus, Tapirus and the Rhinocerontidæ.
    $\ddagger$ Proceedings Amer. Philos. Soc., p. 223.

[^6]:    * Proceedings A cademy Philadelphla, 1874, p. 149.
    $\dagger$ Report Expl. Surv. W. of 100th Mer. U. S., G. M. Wheeler in charge, iv, pt. ii, p. 349, 1877.

